

The nesting activities of the vespoid
potter wasp *Eumenes campaniformis*
esuriens (Fabr.) compared with the
ecologically similar sphecoid *Sceliphron*
madraspatanum (Fabr.) (Hymenoptera)

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(With two figures)

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DAUBING

All individuals of both species added a number of loads of mud to their constructs after they had completed and sealed a cell. These can be classified in various ways. In our previous paper on *m1* we used the word *daubing* and often used the metaphor 'roughcast'. Other authors have adopted Roubaud's (1916) word *crépissage* which may be translated by roughcast, but has been adopted into entomological literature in English because it has a wider range than any translation. In this paper we are using both words and giving them separate meanings. *Crépissage* in the present sense is only constructed by *esuriens* and other species of *Eumenes* that we have seen Jayakar & Spurway (1965). Its structure is physically different and, as shown in Table 11, it is worked at a different tempo from the daubing proper which is similar in form in both species, and it is laid down in a special context. *Crépissage* will be considered more fully in the next section.

All wasps observed, when they had sealed a cell, laid down some loads of mud not clearly associated with the lid or with the site of the next cell. These loads were carried and put down in the manner characteristic of the species. The *madraspatanum* wasps first put down the loads and gradually spread them out so that their final form was like a little cow-dung cake drying on a wall for fuel. The *esuriens* wasps again held their loads clear of the construct and spread out the mud

from only that part of the load with which the construct had been touched, so that one load was frequently divided between several sites.

In both species daubs were usually placed in chinks between two cells, and between cells and the substrate, and their function could often be appreciated. However, the number of such loads put down by members of both species was very variable. Sometimes only one or two such loads were brought between building two cells and the daubs made with these would be quite inconspicuous in an excavation of the finished nest. The wasps *m3*, *m4*, and *m5* made few daubs before making the foundations for the next cell. The result of variation in the number of loads put down seems similar to a nest variation reported by Roubaud (1916) in the Vespoïd which he calls *Synagris callida* L. but which Wheeler (1923) states is correctly *S. spiniventris* (without an author). The nest made by *m1* corresponded accurately to Roubaud's description of a *compact* nest in that species, whereas *m3*, *m4*, and *m5* made what would be called *dissociate* nests. This difference, which we regard as quantitative, Roubaud believes to be determined by the consistency of the mud used. Wasps *e1*, *e2*, *e5*, and *e8* also differed similarly among themselves, only *e2* resembling *m1*. Their daubs were spread much thinner and more smoothly blended with each other and with the previous construct than those of *madraspatanum*.

While daubing, both species of wasps put loads of mud, not only on the construct, but also on the surrounding substrate. The working of these loads was, for both species, quite deliberate, but quite different, and in both the function is at best controversial. Wasps *e2* and *e5* occasionally, and late in their work, laid down a load either entirely separate from the main part of the construct or as discrete patches or blobs extending out from it. These may be considered as the beginning of crépissage and will be considered later. They were also made by less systematically watched wasps. On the other hand, *madraspatanum* wasps spread out mud with movements indistinguishable from those with which they made foundations but in regions where cell walls could not have been built without occluding the opening of previous cells. Some of such *smoothings* by *m3* did not join the cell block; Dutt (1913) has also described these. They may have a camouflaging function (Horne 1872).

We have so far considered daubing (in our sense) and associated activities that were performed after a cell has been closed. These may be called *in phase* daubing. Concerning *out of phase* daubing, *m1* only daubed one load at any other time and this was between two loads used to make cell walls and was related to the walls of the cell being built. The *esuriens* wasps more frequently alternated daubs and walls at the beginning of a cell. These daubs are considered to be part of the series of *in phase* daubing which had preceded the wall building. However the

esuriens wasps appear to daub at least two other times, and under other stimuli. Wasp *e1* followed oviposition in the two cells we watched with a period of daubing before provisioning which did not extend on to the newly built cell. These were calm and though each was preceded by a relatively long absence and at least one loadless inspection, they seemed to have the same function as the daubs she added after sealing, and in Table 11 and Fig. 9, are grouped with these. Secondly, *e2* produced one period of work, *e5* two, and *e8* three which might be called *panic daubing*. We do not know what evoked this from *e2* but her behaviour left little doubt that she was dealing with a crisis. After inserting the fourth larvae into her cell V, *e2* did not leave, but hovered and landed twice. She then brought ten loads of mud most of which she put down on the two most recent cells. She worked more quickly than previously (Table 11 and Fig. 9) and also deposited water on the construct while doing so. She then resumed provisioning cell V. Judging by this behaviour, it seemed that the crisis was caused by the construct becoming defective. Over two and a half hours before, while building cell V, *e2* had spent an unusually long time feeling the construct.

On the two occasions when *e5* daubed *out of phase*, the wasp was almost certainly aware that another insect had been near the nest in her absence. Similar incidents preceded the final closing of nests of this and other species (Jayakar & Spurway 1965, and below). Therefore we suggest that the presence of an enemy stimulates or releases this activity. This is suggested by the following observation: On 19/10, an individual of *Chalybion bengalense* landed on the construct and swept the newly finished mouth of cell *e5* IX with its antennae for four seconds before flying away. It thus can be assumed to have left some scent on the nest. However *e5*, who was first noticed 113 seconds later, and who approached hesitatingly, and from an unusual direction, may have seen it on the nest. After appearing reluctant to land, *e5* landed and examined the nest for over 5 minutes, left for over half an hour, returned without a load, and examined for 6 minutes. She then daubed 16 loads followed by an inspection visit and left for the day. Next morning, after the first loadless inspection visit, she provisioned cell IX normally.¹

On 24/10, while *e5* was making the neck and lip of cell XII after nearly an hour's delay due to rain, a blue-green cuckoo wasp of the family

¹ Our interpretation of this behaviour of *e5* suggests that *C. bengalense* has, for potter wasps, some stimuli similar to those produced by chrysid cuckoo wasps. The closely related *C. californicum* is believed to open cells of *Sceliphron cementarium* and remove the wasp larvae and provisions before using the cells for rearing its own young (Meeusebeck *et al.* 1951, Evans 1963). *C. bengalense* is certainly a squatter, and we have seen individuals empty the provisions out of holes in wood recently filled by themselves, by other members of their own species, and by other squatters. Vespoid squatters also behave similarly. *C. bengalense* also collects mud for sealing its own cells from the nests of potter wasps and from the lids of squatter wasps, and may, therefore, open their cells while these are still occupied.

Chrysididae examined the abortive foundation built by *m2* 27 days before. This smear of mud was about 48 cm. vertically above cell XII of the nest of *e5*. The chrysid was chased away by the observers before *e5* began ovipositing. After this, instead of provisioning, she immediately daubed 13 loads of mud before work was interrupted by failing light.

As for *e8*, we are unable to understand why she daubed out of phase when she did. On 17/4/63, in the middle of making the walls of cell VIII, she put down 6 daubs in several different places. Then, on the next day, having finished her cell IX and laid an egg in it, she left at 11.56.51. At 13.27.36 she returned without a load, inspected for 74 seconds, and then fetching mud in another 242 seconds, she had a spell of daubing during which she brought 10 loads of mud. The only other visit she paid to the nest that afternoon was an inspection visit. There was some rain that afternoon. On 20/4, also, after ovipositing in newly finished cell XI, she left at 13.48.43. At 14.26.42 she returned loadless, inspected for 103 seconds, was away for 582, at the end of which she brought 7 loads of mud which she daubed, then remained away for 3133 seconds, returned loadless, inspected for 140 seconds, made 4 more daubs, remained away for 2929 seconds, returned loadless for 32 seconds, then daubed 4 loads and left for the day at 16.47.45. During this panic daubing, the clouds had been increasing.

Table 11 and Fig. 9 (below) make clear that all wasps increased their speed of work while panic daubing, and where data are available, i.e. for *e2* and *e5*, these speeds were not significantly different from those at which they built their final crépissage. Three *esuriens* (*e13*, *e22*, *e23*) made structurally unmistakable crépissage before returning to cell construction. We do not know the contexts in which this was made.

THE FINAL FORM OF THE CONSTRUCTS INCLUDING CRÉPISSAGE

Column 10 of Table 1 describes the condition of the material construct when the nest was left. For many nests we have evidence, either direct, or from the accumulation of prey, that the wasp had visited the construct after the last load of mud had been deposited. This is the date entered in column 9 of Table 1 and used in constructing Table 9. From these data, we find that 2 or 3 *esuriens* and 3 *madraspatanum* wasted some labour and at least 12 *esuriens* and 2 *madraspatanum* not only wasted labour but left an offspring partially or completely unprovided for. A young wasp in an unsealed cell is not certain to perish, though *e16* I was both abnormally small and unable to emerge from its pupal skin. Wasp *e9* I, unfortunately, was killed 24 hours after emergence from the pupal skin. At the time it was judged to be deformed but

the observation made later that *esuriens* imagines do not assume their adult posture until at least 36 hours after emergence from the pupa makes this interpretation almost certainly erroneous.

Before we discuss whether these 19 desertions are to be considered involuntary, i.e., the mother being prevented, probably by death, from returning to the construct, we will consider how the remaining 11 nests were left. They were all constructed by *esuriens*. In 5 (*e7*, *e13*, *e15*, *e19*, *e24*) the last cell was sealed, and in some certainly daubed a little in the way previously described. The remaining six *esuriens* (*e2*, *e4*, *e5*, *e6*, *e14*, and *e22*) made the qualitatively different style of daubing to which we wish to restrict Roubaud's (1916) term *crépissage*. This structure was begun by all except *e4* and *e14* only after the sealing of a cell; in these two it was begun while a cell was not only unsealed but completely unprovisioned containing only the suspended egg, so these two individuals must be added to the previously mentioned 19 who wasted labour and abandoned an offspring. The wasps observed built their *crépissage* by working with increased intensity, fetching mud more quickly (Fig. 9 below), working it more rapidly on the nest and, at the end, hardly spreading it out at all. Table 11 compares the various types of daubing for the different wasps with regard to time spent on the nest while working a load. *e2* and *e5* also divided a single load between more and more sites, the maximum being five. Therefore finished *crépissage* has a crumbly or granular surface and must have a porous consistency (compare Fig. 7 with Fig. 8). The wasps also made ribbons of mud on the substrate. These were slightly rucked and resembled the ribbons made by pushing the paste made of icing sugar through a funnel while decorating a cake. These ribbons were often continuous with ridges over the cells, but some were entirely separate from the main construct. The wasps also constructed vaults extending over many cells. These were constructed from ridges and ribbons which were added to so that they curved over enclosing a considerable amount of space. A vault could be constructed from one, two, or three ridges joined up in an elaborate manner which was sometimes symmetrical and sometimes not. The open lips of the last cell of *e4* (IX) were joined up and made continuous with this vaulting, as were those of cell *e22* VII which had not been destroyed when the cell was sealed, perhaps precisely because the wasp had determined to build *crépissage* immediately afterwards. Iwata (1942) considers these vaults to be an adaptation to minimise fluctuations of temperature within the cell by surrounding it with an air jacket. We suggest that they may also provide a defence against cuckoo wasps. Wasp *e14* put on two complete layers of vaults, and included her open cell within them whereas *e2* and *e5* only made one small vault each.

We have compared such a completed *crépissage* (Jayakar & Spurway 1965b) to a miniature chain of recent mountains with smaller ridges

extending from a central spine. Only four wasps (*e2*, *e5*, *e6* and *e14*) closed their vaulting, and the first three of these, to continue the mountain metaphor, built up the peak over their youngest cell (which, only in nest *e5*, was the highest vertically) into a little pinnacle approximately 1 cm. high, and therefore somewhat destroying the resemblance of the construct to a mountain range by being so grossly out of proportion. In detail this pinnacle resembled a small cairn of stones, the mud balls of which it was made being barely worked into one another at all. The function of this cairn is unknown. Wasp *e5* almost invariably landed on hers once it was constructed. We have seen no comparable structure to this cairn constructed by *E. emarginatus conoideus* or *E. p. pyriformis* (Jayakar & Spurway 1965b).

The only *esuriens* for whom we have data (*e5*), fetched all the mud for her crépissage from the same source as she used for her cell walls, and the colour of the crépissage of the other nests confirms that, for our population at least, this is so far the rule. In this *esuriens* again differs from *conoideus* and *pyriformis*, who in our experience have completed, almost decorated, their crépissage with material of a different colour and consistency from the material of which their cells and the bulk of the former were made. Finally, *e5* and *e22*, who were still working on their crépissage when their earlier cells were due to emerge, left these earlier cells uncovered. We have recorded the same omission by *conoideus* (Jayakar & Spurway 1965b).

As a routine we continued watching the nests of *e1*, *e2*, *e5*, and *e8* during the hours of daylight until the wasp had failed to return for 24 hours (20 hours 24 minutes for wasp *e2*). We thus watched *e2* and *e5* withdraw from their constructs after they had finished building them to their own satisfaction. Their remaining visits were loadless and are given below :

<i>e2</i>		<i>e5</i>	
away	on	away	on
256	10	10621	4 ¹
4856	2	4183	13
8833	10	76086 ²	27 ³
73462 ²	watching discontinued	87644 ²	watching discontinued

¹ hovered over sill before leaving.

² including a night.

³ including hovering over nest.

The function of these returns after long intervals (also recorded for *conoideus* and *pyriformis*) is not obvious ; perhaps they have no function and are the inescapable consequence of the evolution of *both* a memory and a positive reaction to the nest, neither of which disappears abruptly.

The capacity to make these visits may make various adjustments possible in rare catastrophes, and it may have important evolutionary significance.

If we consider closed vaults, and perhaps a cairn, as evidence for a completed construct, we imply that no *madraspatanum* and only 3, or perhaps 4, *esuriens* completed their constructs, though it is probable that *e22* would have done so if the nest had not been dissected on 18/6/64. Beginning with the animals we watched at work, we will consider the circumstances that stimulate a wasp to cease cell building and begin crépissage, and discuss the evidence that similar stimuli may precipitate desertion.

After *e1* had left, having put down her second load of mud onto her cell IV, a chrysid cuckoo wasp landed on the nest. She was attacked by *e1* and they both flew off together. The cuckoo returned and laid an egg through the wall of cell II with the mother hovering over her. The movements of *e1* were frightened, not aggressive. The two wasps then left together but the cuckoo returned in 6 seconds and inserted her abdomen. *e1* returned in 198 seconds but was temporarily prevented from reaching the cells by an unsuccessful attempt to catch the cuckoo. The cuckoo left, returned, and put her ovipositor into I. When the chrysid left, *e1* returned. We do not know if she had been around all the time. She inspected the cells for 11 seconds. She returned two more times for 8 seconds and 2 seconds after intervals of 15 and 27 minutes respectively bringing no loads, merely inspecting the cells. After an hour, a chrysid of the same species again appeared on the cells. That she concentrated her attention on cell III does not prove she was the same individual, as she could perhaps have recognised, by the visible little pits in their walls, that cells II and I had already been parasitized. She laid in III, and was captured. Nearly half an hour later, i.e. after she had been away 50 minutes, *e1* returned again without a load and inspected for 5 seconds. She did not return during the next 24 hours of daylight, i.e. she apparently deserted because all her cells had been parasitized.

The panic daubing performed by *e2* during provisioning of cell V has previously been described. On the same day, after sealing cell V she immediately made an inspection visit and then brought 15 loads of mud, 14 of which she daubed during periods on the nest ranging from 14 to 32 seconds. The last load she dropped, most probably because she saw the approach of a chrysid. This cuckoo was most persistent in her attempts to lay but was finally captured by us. *e2* returned with mud and it was soon after realized that her building was different from any previously seen. Though between sealing one cell and beginning the next, *e2* always made more than 20 daubs, usually more than 30, the speed with which she worked the 14 daubs immediately after sealing V suggests that these were crépissage daubing. If this is correct, the

beginning of this *crépissage* was not stimulated by the presence of the cuckoo. The decision to close the nest may have been due to the stimuli that provoked the panic daubing during the morning.

On two occasions when *e5* brought larvae to cell XIII, a striped fly, probably a sarcophagine and similar to those which parasitized *e8* and *m3*, followed her across the verandah and settled on the window sill facing the nest. As soon as *e5* had left, the fly flew to cell XIII and put its head in. On both occasions it was disturbed by the observers. On neither occasion did *e5* do any feeling that could be interpreted as reacting to the fly's foot prints as she had reacted to the *Chalybion* 14 days before (p. 151). However, after the second occasion she made an inspection visit, sealed her cell and began her *crépissage*, again immediately, judging from her speed of work. Wasp *e5* roughcasted the earlier cells very much less than the later so that their surfaces remained smooth and only the upper half of the construct assumed the crumbly texture (see Fig. 8). This seemed a deliberate response to the demands of the situation. Is it possible that the wasp knew that her earlier cells contained offspring too advanced to be vulnerable to parasitization? Or, to use a somewhat pedantic jargon, why did these early cells not provide the stimuli for *crépissage* or, alternatively, provide stimuli inhibiting it. The first emergence, that from cell II, took place while this final rough-casting was being performed.

Wasp *e8*, who had not reacted to the presence of a fly which, on 17/4/1963, had successfully oviposited, or perhaps larviposited in cell VII, deserted on 21/4. On 20/4, she oviposited in cell XI at 13.48 after completing the building of that cell. At 14.26 she returned without any load, which in itself was not surprising, but what followed was. She spent 103 seconds feeling the construct, than left, and returned after 582 seconds with a load of mud and daubed it on the construct. She brought 7 such loads and was then absent from 14.48 to 15.40 when she again came without a load. This time she spent 140 seconds on the construct of which she spent 63 seconds absolutely quiet with her head over the mouth of cell XI. She left and then returned for a second stretch of *out of phase* daubing. This time she brought 4 loads. She was absent from 15.50 to 16.40 when, after another inspection of 32 seconds, she did some more daubing (4 loads). The next day she started work at 07.35. She brought 2 larvae, made one inspection and then brought a third larva (at 11.41), until that time behaving quite normally. It was only when she brought her fourth larva that we noticed any change in her behaviour. After putting this larva in within 5 seconds of her arrival, she spent 736 seconds on the construct, for 638 of which she stood over cell XI, quiet except for opening and closing her wings. She left at 11.53, brought her next larva in 154 seconds, spent 168 seconds on the nest, flew away rather suddenly at 11.58 (perhaps frightened by a

house sparrow), returned at 12.44 without a load, and spent 50 seconds on the nest. She returned again with a larva at 14.40, spent only 9 seconds on the nest, and that was the last we saw of her. What the reason, or reasons, were for this unusual behaviour we do not know, but once again desertion was preceded by a marked disruption of the wasp's usual sequence of activities. It is possible that there had been parasitization by an organism such as a chalcid too small for us to notice its entry.

Concerning the *esuriens* nests watched in less detail, we know nothing about the desertion of the nests built by *e7*, *e9*, *e10*, *e12*, *e13* (who had made some crépissage before returning to pot building), *e16-21*, *e23* (perhaps interrupted by observers because emergence had begun), or *e25*. The last certain visit of *e11* was followed by six days of almost continuous rain, and though *m4*, building at the same time, returned and continued her nest, it is not surprising that any given wasp failed to do so after so long an interval.

For the others we have some observations which will now be listed.

Wasp *e3* built one cell, presumably laid in it, and inserted at least three larvae, one a caterpillar and one an apodous larva. Within three minutes of the mother leaving the nest, ants had begun to remove these larvae. They also apparently removed the egg. The wasp was never seen at that site again. It is surprising that other nests were not similarly plundered as there were several ant colonies on the same verandah and individual ants ran in and out of several cells.

Between 11.28 and 11.43 on 11/10/62, cell VIII of *e4* was sealed and two beginnings of cell IX were made. The second of these was completed and laid in at 12.01. During this building, a chrysid was seen flying in the hole in the parapet. It did not land. At 12.03, *e4* returned with mud which she put between cell VIII and the just finished definitive cell IX, beginning her crépissage with a vault. An hour later, *e4* had laid out rows of mud on the wall separated from the cells, and begun to build these up into vaults. At 13.27 a chrysid was found ovipositing, watched by *e4*. Both wasps settled and inspected (not together) and *e4* only resumed building at 13.33. At 15.43 a chrysid was again laying, again watched and not disturbed by *e4*; *e4* was not seen again and no further mud was added to her construct. A third egg was laid by a chrysid next morning at 08.08. When the nest was deserted the nine cells were almost covered by a series of overlapping vaults. *e4* was working on the already continuous edge of the only open hole when the first two chrysid eggs were laid. They were laid within this hole, i.e. into cells and not through the vault roofs into the empty spaces in the crépissage. The overlapping vaults of the crépissage were smooth on the outside and resembled closely the overlapping cells whose contours they masked. Cell IX had not been sealed and the false walls had been joined onto its lip. One vault cut

across the abandoned half-built cell IX, one of its brackets being enclosed and one left outside.

Wasp *e6* was painted at 14.38 while building her cell II. She stopped the moulding she was doing, left, and brought no more mud until 09.03 next morning. Though at 10.16 the cell was found completed, she was found ovipositing in it at 11.02. At 12.02 she was sealing this cell and by 14.02 had completed her *crépissage*, which contained little vaulting. This was extremely rapid work, and the wasp that emerged from cell II was small.

Wasp *e14* was exposed to both stimuli. At 12.58 she was painted on the abdomen while making cell walls. She had finished that cell (VIII) by 13.18 and was daubing. At 14.11 while she was still daubing a chrysid was hovering over the nest, and by 14.41 the *crépissage* was in an advanced stage with an elaborate series of vaults begun. Though these vaults were closed the same evening, the wasp added to her *crépissage* next morning but left without adding a cairn.

The nest of *e15* was only discovered at its moment of desertion when the presumed mother was watching a chrysid depositing her eggs. No further additions were made to the nest.

Wasp *e22* was captured while daubing at 13.29 on 14/6 and painted under ether. On the morning of 15/6 she constructed some *crépissage* including a vault before building her next cell (VII). This she did not seal until 17/6, and when this was discovered, *crépissage* was already begun and a chrysid was laying in the construct having made at least six holes. On the morning of 18/6 the construct was dissected because the wasp from cell I had emerged. The vaults were not yet closed and, as *e22* was working late the previous afternoon, it is probable that she would yet have completed them if she had not been interrupted.

Wasp *e24* hovered while a sarcophagine fly landed and felt the mouth of her cell II on 13/6. She provisioned this cell, built cell III (interrupted in order to etherise and paint), provisioned and closed it, and deserted. When found, all three cells had the small pits left by chrysid oviposition, mud had been dug out of the nest walls, and a mud load was lying near, as though dropped by *e24* while agitated.

From these anecdotes, we consider both that the wasp's behaviour is altered by stimuli provided by the parasite (or perhaps labour parasite), and by her egg holes, and that one very important function of the *crépissage* is protection from such parasites. The presence, or past presence, of a parasite to which a wasp visibly reacted, stimulated her to cease work on her cells, sometimes abruptly, sometimes after the next closure, and to consolidate those she had already sealed. The overlapping walls of the vaults in the *crépissage* completely obscure but *mimic* the overlapping cell walls which they cover, and the spaces within them would trap and starve harmlessly any parasitic egg that was laid into them. Wasp *e4*

did not crépissage cells which had been so parasitized and *e5*, *e13*, and *e22* (and a *conoideus*) left uncovered their earlier cells in which perhaps pupae were not vulnerable to this form of parasitism, as the full grown larva is known to be. Finally, on those occasions when the observers believed that all cells had been parasitized, the mother wasp showed initial confusion from which she recovered by deserting the construct. The chrysid's themselves examined partly finished crépissage. They always laid inside open vaults if possible, and also did not lay inside cells which had already been parasitized, at least by members of their own group. Two species of chrysid, *Stilbium cyanurum splendidum* F. and *Chrysis orientalis* Guer., and the dipteran *Pachyophthalmus auriceps* Baronow have emerged from cells made by *esuriens*.

We have no data which can be used to compute frequencies of parasitization in these species in this locality. Not only have we frequently driven away parasites from nests which we were watching, but the care taken of the nests after they were built was not standardised. Some were caged immediately, some were dissected after varying intervals, while others were exposed until emergence of the oldest offspring had begun, and consequently frequently parasitized long after desertion by the mother.

We have described elsewhere the enigmatical behaviour of *m1* the morning before she deserted her nest. Wasp *m3*, *m4*, and *m5* left their constructs in a similar condition and we have no evidence as to what stimulated this. Dutt (1913) states that *madraspatanum* wasps build all their cells and then roughcast the whole group together, i.e. that they make a crépissage. This has not been performed by any of the wasps we have watched, nor have we found any nest presumably of this species in which all the cells were roughcast¹, and it is rare to find one without evidence of unfinished work i.e. an unfinished or open cell, or one sealed with a concave lid indicating that provisioning was incomplete. We have noticed that the behaviour patterns of these two groups of mason wasps are often confused in the literature, a behaviour pattern peculiar to one being stated to be performed by the other, e.g. by Frost (1959).

Finally, the desertion by *m2* of a site on which she had not built should be put on record. We have described how *m2* selected this site. Including her first visit with mud, she made 15 more visits on 27/9/62, on nine of which she brought mud and smeared it on the place she had selected. She disappeared for the day at 12.44. On 28/9 she made 3 inspection visits beginning at 07.59, being away for less than half an hour

¹ Note added November 1967: of the 13 individuals of *madraspatanum* in our records, one at Bhubaneswar, *m7*, deserted her construct after covering it with a layer of unusually rough daubing. She was painted, and therefore recognised subsequently. She therefore confirmed Dutt's observation.

between them. She was then away for just over two hours and then returned with a large untidy black load certainly not mud and plausibly a spider. She landed for 3 seconds only, then hovered 3 times approaching her mud, flew the whole length of the verandah and returned leaving from the extreme west. No further visits were paid to the smeared mud. Next day a *S. madraspatanum* was seen examining non-homologous parts of the frame of (5), and an individual was seen again on 9/10.

This last visit of *m2* (on 28/9) to the mud smeared by her was clearly a *mistake*, and her uncertain movements confirm this. However, was it a failure of memory or the miscarrying of an instinctive cycle? Did she (as a human might) temporarily forget that she had deserted this site and return to it instead of the later chosen site, where (we are suggesting) she had a cell open to receive the prey; or was she having difficulty finding mud (she took longer to fetch this than *m1*), so her 'building drive' had been superseded by a 'provisioning-drive' without the cell being built, and did the traumatic experience resulting cause the site to be abandoned? There is one piece of evidence suggesting the 'failure of memory' explanation. Before this visit *m2* was absent 7479 seconds. The longest absence after which *m1* returned with a spider was 6106 seconds and this was exceptional; *m1*, at least, behaved as though she was likely to forget the condition of her construct if she was absent for much more than half an hour, and had to make an inspection visit before she could resume work. Therefore we think that *m2* must have been working at some unknown site during these 7479 seconds.

INSPECTIONS AND MEMORY

All the *esuriens* watched in detail (except *e8* on 1 occasion) made a loadless inspection visit in the morning before bringing any load. On the one occasion *e8* did not do so, she had however hovered for 30 seconds in the vicinity of the nest without landing. Chores that did not necessitate a load could be done on these visits, e.g., *e5* laid eggs on the first visit of a morning and *m1* removed concave lids, in both cases after prolonged antennal feeling of the construct. Both wasps sometimes performed these chores on a later visit, but in both cases always before any load had been brought during that day.

Apart from these visits, all the wasps made several inspection visits, mainly during provisioning, and *e1*, *e2*, *e5*, and *e8*, between them made only 10 that were during other activities. The times spent away from the nest before such inspection visits and the times spent on the nest during such visits are summarised in Tables 12 and 13. We suggested that these visits made by *m1* were due to failures of her memory, so that she had to check what her next activity was to be. There is much more overlap in duration between the periods before a loadless visit and one with prey

in the *esuriens* wasps observed (compare Table 6) i.e. on this interpretation they have more variable memories than *m1*, and, as is shown in the tables,

TABLE 12

TIMES SPENT AWAY FROM NEST JUST BEFORE AN INSPECTION VISIT

	<i>m1</i>	<i>e1</i>	<i>e2</i>	<i>e5</i>	<i>e8</i>
no. of timed absences ..	82	3	22	25	23
shortest period ..	40	1006	4	7	1896
longest period ..	7018	4661	6054	8027	6722
mean ..	1878.5	2532.3	1403.2	3039.9	3681.2
median ..	1658	1930	169.5	2756	3324
Q- ..	809		8	562	2743
Q+ ..	2127		2210	4134	4674

Visits after a night absence and visits after desertion of the nest are omitted.

TABLE 13

TIMES SPENT ON NEST INSPECTING

	<i>m1</i>	<i>e1</i>	<i>e2</i>	<i>e5</i>	<i>e8</i>
no. of timed visits ..	90	3	26	25	22
shortest period ..	8	20	2	4	5
longest period ..	917	34	63	108	140
mean ..	87.13	27	16.96	39.68	48.00
s.e. mean ..	14.00	..	2.95	4.97	9.08
median ..	42	27	10	35	38
IQR median % ..	156	..	186	88	165
C.O.V. % ..	152.6	..	88.7	62.7	88.7

For *e1*–*e8*, oviposition visits and first visits of the day have been excluded, as they were clearly longer.

longer ones for this activity. The longest absence before bringing mud was by *e2* and was of 2441 seconds compared with 1863 seconds by *m1*.

Some inspections were made by *m1*, *e1*, *e2*, and *e5* after the wasp had been prevented from working by a spell of rain which interrupted building and all other visits of both species, though *m1* once arrived during a slight drizzle and *e5* once flew into heavy rain after waiting on the construct for an unusually long period and hovering in the verandah before she left. All mud users which we have observed avoid rain, unlike members of the paper-making social species *Polistes olivaceus*, whom we have seen flying into rain so heavy that they were repeatedly buffeted out of course for the best part of a metre until they gave up and returned to the comb. Because of the wasp's avoidance of rain, it is possible that *m4* made the longest absence recorded even though her work was not continuously

observed. At 12.17 on 21/10/63, when cell VII was $\frac{2}{3}$ complete, rain began. She was not seen again until after 13.17 on 27/10 when cell VII was found completed, the mud on the newly made third of the cell being still wet. The morning of the 27/10 was the first time the sky had ceased to be overcast, and rain had been almost continuous since midday on 21/10. Such weather conditions gave her very few opportunities to make a visit and, as the cell was unfinished, these, if made, must have been loadless. The continuously-watched *e5* also ceased all building activities for almost seven days during similar weather in the last week of October the year before, but intermittently brought prey to cell XII which was open. The 1963 rainy period also interrupted *e11* in the middle of provisioning cell V. No further prey were added, nor was there any other indication that the wasp had returned to the construct. Therefore, for the long periods when the absences are certainly due to external causes, there is no indication that one species has a better memory than the other.

There were some inspection visits at the end of the day in both species. On some occasions when a parasite had been on the nest, the *esuriens* seemed very agitated and made several long inspection visits, but in these cases the time spent away from the nests were much shorter than for the other kinds of inspections. Because the visits which wasps have made after completing their *crépissage* have been always loadless, we think these are true inspection visits and are not a result of the wasps forgetfully taking their old path after starting work on a new site, in the way we interpreted the desertion of *m2*.

FETCHING OF MUD

E. esuriens had four different activities for which she needed mud : (1) building of the cell wall, (2) putting the lid on the cell, (3) daubing, and (4) *crépissage*. The fact that *e1*, *e5*, and *e8* could use the same load of mud for both building part of the wall and to daub indicates that any differences in the composition of the mud used for the two activities are not of any importance. *e2* and *e5* also sometimes used the same load for making the lid and daubing. In one period of panic daubing, *e2* used much more water for her work.

Iwata (1953) and Olberg (1959) have described their observations on species of *Eumenes* where the wasps drank water on some journeys, took it to their mud patch, and regurgitated it there. Our observations support theirs. For *e1*, we knew the location of the spot where she collected her mud. She certainly did not always get it from exactly the same spot but roughly from within a rectangle about 1 metre by 50 cm. She preferred to get it from the bed of a herbaceous border. We could not trace where she got water from, but we know that on some journeys

she did not go to her mud patch which was about 5 m. from her nest but went away to the west, probably to the leaking tap of a neighbour's garden which was about 50 m. away.

The other wasp for whom we have information is *e5*. This wasp got her mud from dry caked soil in exposed rough ground about 27 m. south of the nest and her water from a leaking tap about 50 m. to the east of her nest. By the time *e5* had built 4 cells (i.e. 13/10) her mud patch had narrowed down to a very small area, and after that she always collected from a roughly circular patch about 30×30 mm. and at that time about 4 mm. deep. She collected all further mud from here and, half way through her *crépissage* on 2/11, her quarry had narrowed to a pit 10 mm. deep but only 20 and 15 mm. in diameter. It had by then been exposed to heavy rain and hence standing water.

The wasps did not, however, need to fetch water on every journey. They could bring water in their crops sufficient usually for two loads but on occasions even for 3 loads. However we do not know where the wasps went on each of their absences. Fig. 9 shows the distributions of times spent by the wasps in bringing mud for different activities. As one would expect, it takes a wasp a longer time on the average to fetch water and mud than it takes her to fetch mud alone. This is reflected in the bimodalities in several graphs e.g. those for *crépissage* by *e5* and cell building for *e8*. The time spent away should therefore indicate whether a wasp went on a 'water+mud' journey or a 'mud' journey. But, unfortunately, the 'noise' is so much that there is considerable overlap and these two types of journeys cannot be sorted out by the time spent on them. The unexpectedly long intervals, some of which have been excluded from the graphs, are probably journeys on which she was either disturbed or on which she fed. Table 14, however, gives the distributions of times spent

TABLE 14

COMPARISON OF TIMES SPENT ON FETCHING MUD ONLY WITH THOSE SPENT ON FETCHING WATER AND MUD

Object of journey	No. of journeys timed	Range (in secs.)	mean	variance
Fetching mud only	30	50-121	73·20 ± 3·37	634·2
Fetching water+mud	6	100-168	144·17 ± 10·28	340·9

for those journeys throughout her construction when we actually saw *e5* going straight to mud or straight to water. (On some occasions when there had been rain *e5* did not go to her usual supply of water at all but flew around a herbaceous border. We never actually saw her collecting water accumulated on the leaves of the plants, but suspect that she did).

Concerning *S. madraspatanum*, *m2* only brought 9 loads and she took considerably longer to fetch them (mean time away, 225 ± 91 seconds; range, 116-402 seconds) than either *m1* or the various *esuriens*. When *m1* fetched mud, she not only made a choice of several directions when she departed, as did the *esuriens* wasps, but unlike them, she could also return from one of several directions. Nevertheless her times away were remarkably constant. When these were classified into the use made of the mud some small but significant differences were found between the times taken to bring mud for different functions. About 10 seconds longer (or 25-30% of the time away) was taken to fetch mud used for the finer work. We previously interpreted these figures as revealing that *m1* may either have worked the mud for some purposes longer while collecting it or may have chosen some mud more carefully i.e. have had different collecting sites for different purposes. We watched *m4* collecting her mud to build cell walls. It was scraped with the mandibles, rolled with the front tarsi, and carried in the mandibles. The wasp buzzed during this work as she did while building. Her source was about 38 m. from her nest in a small hollow eroded by the drain from an outdoor bath tap. The soil was slightly soapy but not smelly. She had a stereotyped route of about 40 m. going round the house, and we never saw her either collect water or make any detour suggesting that she did so. Her collecting spots were all within 1 cm. of one another and, for example, during the building of one cell, her left hind tarsus was on one particular stone during all collecting we watched. During another period she was delayed by a column of ants crossing her minute quarry. She collected from an adjacent place which she took time to select, but after carrying away several loads she started dropping them without leaving and, after attempting to collect as near as possible to her own site, she finally returned to it when the ants left. She had a stereotyped landing and walked 2 cm. to her quarry. We could see no difference in location or texture between the mud she used for walls and the mud she used for daubs, and thus consider our second hypothesis about *m1* inapplicable at least to *m4*, who resembled *e5* in having one quarry for all purposes.

We have thus failed to confirm Iwata (1942) that *madraspatanum* carries water to its mud patch to damp the mud¹. On the contrary, we have seen *m4* collected mud at a permanently damp place, and, as we suspected for *m1*, any damping would have been redundant. The collecting site chosen by *m4* confirms Iwata (1964) that this species choose relatively dirty mud. The frequent observation of cells filled with mouldy spiders in which no wasp offspring can be found is explained by Iwata

¹ Note added November 1967: We have repeatedly seen the squatter *Chalybion bengalense* Dalb. collect water. This species was included in an extended genus *Sceliphron* by Bingham (1897) and Kohl (1918).

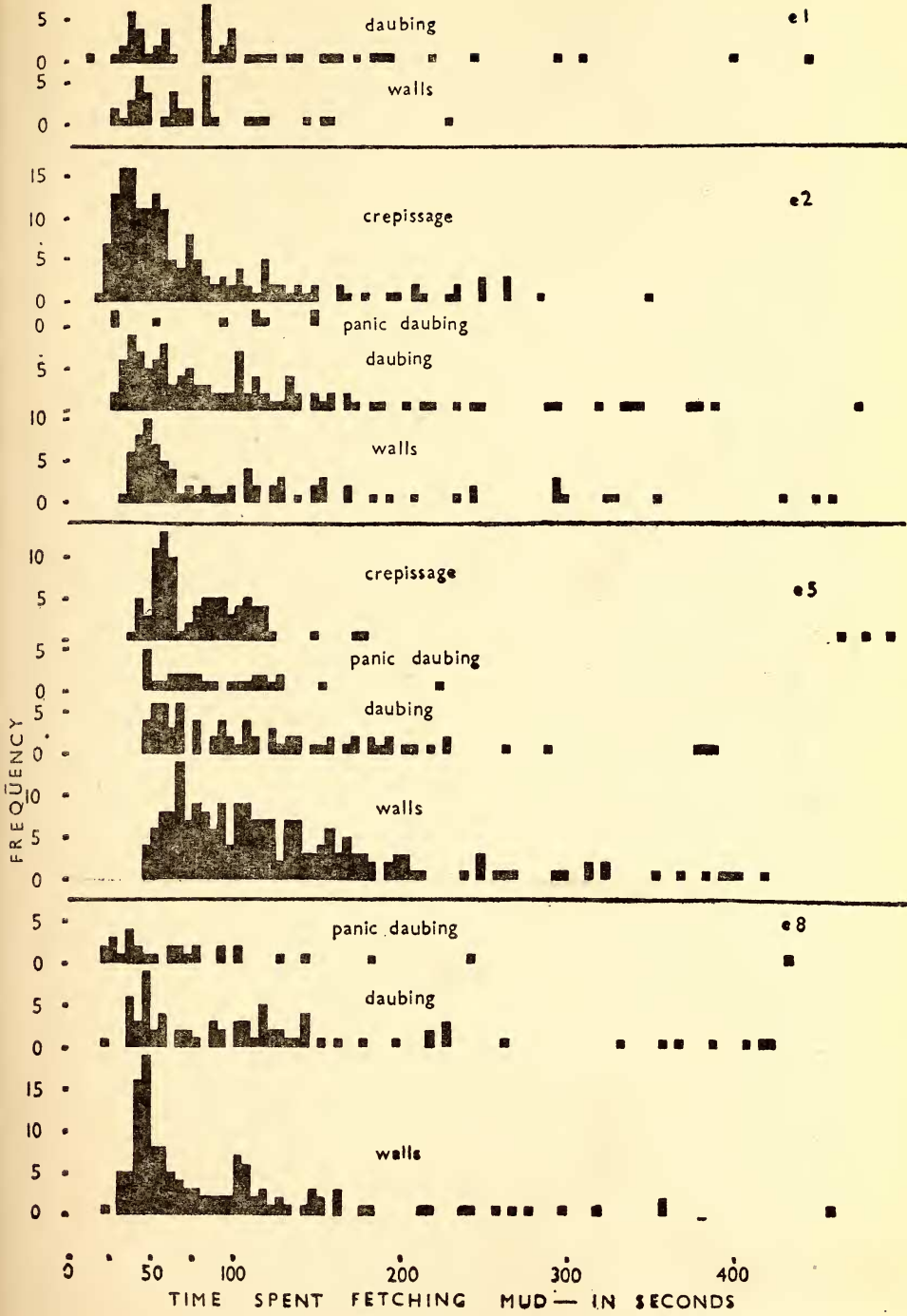


Fig. 9

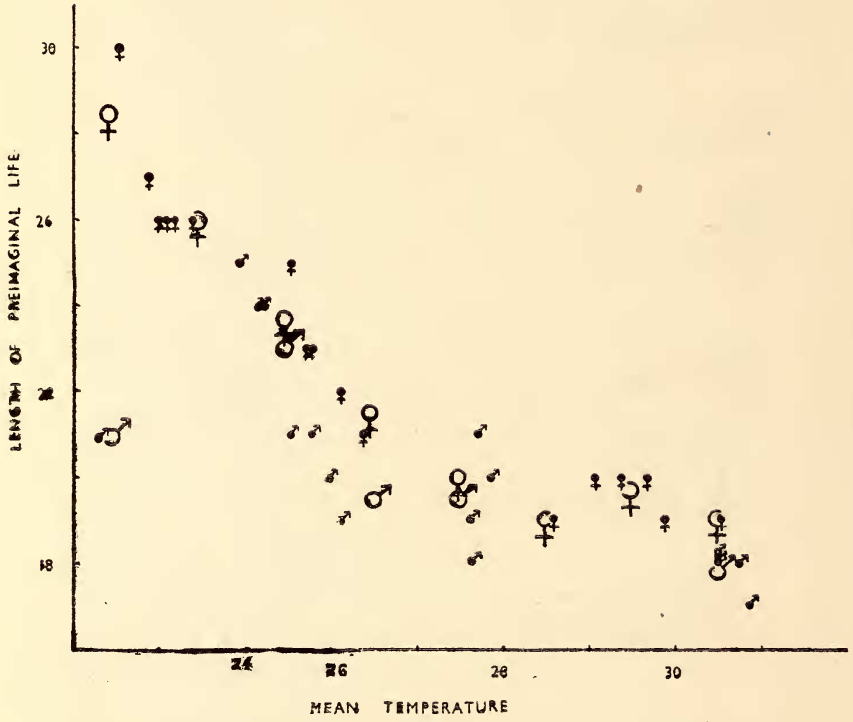


Fig. 10

(1964) as due to the organisms present in the mud infecting the spiders so that these become inedible to the wasp larva, who therefore perishes soon after hatching. While confirming the facts, we are nevertheless sceptical of this explanation, perhaps because of our experience as *Drosophila* workers. Mould does not render a *Drosophila* culture sterile, it only begins to grow in a culture after this has become sterile for other reasons. Similarly we think that mould would not attack paralyzed but still living spiders ; it would attack only after these had died because a wasp larva had delayed or failed to eat them for some other reason.

LENGTH OF PREIMAGINAL LIFE, EMERGENCE AND COCOONS

The length of the period between oviposition and emergence for *esuriens* is very variable. Assuming that the first egg is the functional one, the length of preimaginal life varies, in our sample of 17 males and 17 females, from 17 to 25 days for males and from 19 to 30 days for females. This variation is largely due to variation in temperature during preimaginal life. Fig. 10 shows the relation between length of preimaginal life and the mean temperature during it. (This is the mean of all daily maximum and minimum temperatures during the relevant period). The solid ♂ and ♀ signs represent individual wasps, while the larger open signs represent mean periods for a given temperature range (Table 15). Even such small samples show that development is speeded

TABLE 15

RELATIONSHIP OF LENGTH OF PRE-IMAGINAL LIFE TO TEMPERATURE

Mean Temperature (°C)	Males		Females	
	Number	Mean length of pre-imaginal life	Number	Mean length of pre-imaginal life
23-	1	21.0	2	28.5
24-			4	26.0
25-	5	23.0	3	23.7
26-	2	19.5	2	21.5
27-	4	19.5	1	20.0
28-	..		1	19.0
29-	..		3	19.7
30-	5	17.8	1	19.0
	17		17	

up with increase in temperature. (The exceptional ♂ on the extreme left of the graph is the small e6 II who emerged from a cell sealed only 1

hour after oviposition). It is also clear that females take a longer time than males to develop, and that this difference, where data are available, varies from 0.5 to 1.2 days (excluding the exceptional male e6 II). The only comparable data we have on the length of preimaginal life for *madraspatanum* are those for m1, for all the imagines produced by m4 and m5, except perhaps one, had entered diapause in the larval stage. The variation between individuals was much less, the period being 20 days for males and 20-21 days for female (mean 20.35 days). More data must be awaited before a comparison can be made between the two species.

Wasps that have emerged from their pupae in glass tubes are fully coloured but lie passively in a curled up position for well over 36 hours. The bellies of *madraspatanum* are distended with the white pellets of excreta which can be seen through the intersegmental membranes. This confirms Roubaud (1916) that wasps remain as imagines inside their cells for several days. Certainly they do not emerge until they can walk and fly normally. The typical folding of the vespid wing takes place within two minutes after emergence from the cell.

The imagines of *esuriens* emerged from a hole gnawed in the side of the pot usually facing the source of maximum light. The lids fell off completely and were unexpectedly thin. The lids of *madraspatanum* were even thinner, which was surprising as these were chewed through the convex lid and lid daubing with which the mother had originally sealed the cell. The hole opened had a smaller diameter than the original mouth of the cell, and often the lid was not pushed off by the emerging wasp, but fell back into position lying parallel to the surface of the block and again occluding the hole.

The internal debris in the cells reveals very different larval and pupal organisations. Both species are typical of their taxonomic groups. The inner walls of *esuriens* cells were very faintly silvered as though by snail tracks. This was the only vestige of a cocoon. The larval faeces were deposited as a large yellow or red clayey patch which was adsorbed by the mud of the cell wall. The colour almost certainly depended upon the food. When animals were reared in glass tubes the extrusion of this coincided with the larvae ceasing to be green or yellowish brown, transparent and glassy, and becoming butter-coloured and opaque. Several larvae seemed to drown themselves in their excreta unless some fragment of cell wall or other absorbent substance were present to soak up the liquid. Like other members of their genus (Kohl 1918, Shafer 1949), *madraspatanum* wasps made cylindrical cocoons which, though of silk, had the russet colour and lac-like consistency of a cuticular puparium; The larval excreta formed dense black masses in the proctodeal ends of the cocoons which were sculptured to receive it and thus formed what has previously been called faecal baskets. There is also a butter-coloured

opaque stage after the cessation of feeding and this excretion in *madraspatanum*, and it is in this stage that diapause occurs.

We saw no meconium produced after pupal life in a nest of *esuriens*. It is probable that they void this after flying from the nest as do the social *Polistes*. Shafer (1949) has discussed the development and composition of the little spindle-shaped white pellets of excreta with which *Sceliphron* wasps are full when they emerge from their pupal skin and which they slowly void, both before and after leaving the cell.

SEX RATIO AND BIRTH ORDER

Table 16 summarises the emergences we have observed. As would be expected from our descriptions of the wasps' behaviour, a large number of cells were parasitized but, as previously explained, the data given in Table 16 were *not* collected to give any estimate of the frequency of this in this region. There were other causes of death in undisturbed cells which are not easy to explain, and some larval and pupal deaths were certainly due to the abnormal conditions provided by a glass tube.

The individuals of *S. madraspatanum* were sexed by examining their genitalia and/or their antennae. The individuals of *E. esuriens* were sexed by the presence of a hook-like thirteenth segment on each of antenna of the males. Bingham (1897) listed several pigment differences between males and females in this species. We agree with him that the mid and hind tarsi of males are black, and of females russet. We also note, which he does not, that the antennae of males have a dark band at their most swollen point. The male 5 II whom we only saw for 13 minutes on the nest was sexed on these pigmentary characters only. Bingham also stated that females do not possess two black spots present on the ventral surface of the second abdominal segment of males. About half of our females scored are noted as having these spots, which are however fainter, smaller, and more diffuse than any seen on males.

The sex ratios observed in these samples are exactly 1 in each species. This is surprising, as the order in which eggs are laid is far from random. Jayakar (1963) reported a condition which he called 'protarrhenotoky', namely that during the life of a single female, she lays *all* her male eggs before *all* her female eggs. The data which were available at the time of that publication were those from *e1* to *e6* and *m1*. As can be seen from the data now available, at least in *esuriens*, this rule is not invariably followed. In nests *e8* and *e23*, there were exceptions to this rule; in the former, 1 male egg having been laid after 4 male and 1 female eggs, and in the latter, 2 male eggs having been laid after 3 female eggs. In *madraspatanum* so far, we do not have any exception to the rule.

TABLE 16
CELL CONTENTS

Cell No.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	♂	sex ratio	♀
Nest																
e1	C ♀	C ♀	C ♀	♀	♀	C ♀	C ♀	C) ♀	u ♀	♀	♀	♀		5		5
e2	u ♀	♀ ♂	♀ ♂	♀ ♂	♀ ♂	C ♀	C ♀	C) ♀						2		5
e3	♂	♂	♂	♂	♂									1		7
e4	♂	♂	♂	♂	♂									1		
e5	♂	♂	♂	♂	♂									5		
e6	♂	♂	♂	♂	♂									1		1
e7	♂	♂	♂	♂	♂									1		
e8	♂	♂	♂	♂	♂									1		
e9	♂	♂	♂	♂	♂									4		
e10	♂	♂	♂	♂	♂									2		
e11	♂	♂	♂	♂	♂									1		
e12	d	u	♂	♂	u									4		
e13	e	♂	[S]	[S]	♂									2		
e14	e	♂	[S]	[S]	♂									1		
e15	e	♂	[S]	[S]	♂									2		
e16	(C)	u	[S]	[S]	♂									1		
e17	pu	♂	[S]	[S]	♂									1		
e18	♂	u	[S]	[S]	♂									1		
e19	p	u	[S]	[S]	♂									1		
e20	?	u	[S]	[S]	♂									1		
e21	C	u	[S]	[S]	♂									1		

e22	e	e	♀	♂p	♀p	C	C	♀	♀	u			4
e23	e	e	C	C	C	♂	♂						4
e24	♂	e	C	C	C	♂	♂						1
e25	♂p	e								C	u		2
Total												28	28
m1	♂†	♂	♂	♂	♂	♂p	♂	♂	♀	♀	♀	ul	4
m3	d	d	u	♂†	♂	S	d	♀	S	S			3
m4	♂†	u	♂	♂	♂	u	♂†	♀	♀	♀			3
m5	♂	♂p				♀p	♀	p	♀				5
Total												10	10

Key :

- u cell left unsealed
- C one chrysid wasp
- S several sarcophagine flies
- c several chalcid wasps
- t died before emergence or otherwise imperfect imago
- p died as pupa
- l died as larva
- d debris—not noted for open cells
- e escaped
- ? unknown parasite
- () order of cell construction unknown
- [] cells now continuous because holes had been bored by parasites in the intervening walls.

TABLE 16
CELL CONTENTS

Cell No.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	sex ratio		
														♂	♀	
Nest																
e1	C	C	C													
e2	u	♀		♀	♀											5
e3	u	♀														
e4	(C)		♀	♀	♀	C	C	C	u	♀	♀	♀	♀pc		5	7
e5	♂†	♂	♂	♂	♂	c	♀	♀	♀						5	
e6	♂†	♂	♂	♂	♂										2	
e7	♂	♂	♂	♂	[S	S	S	S]	♀	♂	u				1	
e8	♂	♂	♂	♂											1	
e9	♂u														1	
e10	♂														1	
e11	♂	♂	♂	♂	u										4	
e12	♂	♂	♂	♂												
e13	♂	♂	[S	S]	♀	C	d	C							2	
e14	(C	♂	C	C)	♀										1	2
e15	(C	♂	C	C)	♀											
e16	pu	u	C													
e17	♂	u	C												1	
e18	♂	C	C													
e19	♂	C	C													
e20	♂	C	C													
e21	♂	C	C													
e22	e	♀	♀p	♀p	C	C	♀								2	4
e23	e	C	C	♀	♀	♂	♂	♀	u						1	4
e24	d	C	C	♂	C	C	C	C	C	u					2	
e25	♂p	e	C	C	♂	C	C	C	C	u						
														Total	28	28
m1	♂†	♂	♂	♂	♀p	♀	♀	♀	♀	u					4	5
m3	d	♂	S	S	S	S	S	d	S	u					3	
m4	♂†	♂	♂†	u	u	♂†	p	u	u						3	
m5	♂	♂p	♂	♀	♀p	♀	♀	♀	u						3	5
														Total	10	10

Key :

u	cell left unsealed
C	one chrysid wasp
S	several sarcophagine flies
c	several chalcid wasps
f	died before emergence or otherwise imperfect imago
p	died as pupa
l	died as larva
d	debris—not noted for open cells
e	escaped
?	unknown parasite
()	order of cell construction unknown
[]	cells now continuous because holes had been bored by parasites in the intervening walls.

Arguing from all the *madraspatanum* data where offspring could be sexed, as Jayakar (1963) did for the *esuriens* data, we now compute the probability that if 10 male eggs and 10 female eggs are laid at random in nests of 9, 3 and 8 cells, the rule of all male before all female will not be broken. This probability is $\frac{34}{184756}$ or 1 in 5434.

For *esuriens*, such a test becomes impracticable. The tendency to 'protarrhenotoky' however, is still clearly evident. The data show several peculiarities which are due to this tendency. One is the large number of unisexual broods. Classifying the nests by the number of sexed offspring we have :

No. of sexed offspring	No. of nests	Sexes of sexed offspring
1	5	all ♂♂
2	3	all ♂♂
3	1	♂♀♀
4	2	♂♂♂♂ ; ♀♀♀♀
5	2	all ♀♀
6	2	♂♂♂♂♀♀ ; ♀♀♀♂♂♂
12	1	♂♂♂♂♂♀♀♀♀♀♀

All three nests with 2 sexed individuals, both those with 4 individuals, and both with 5 individuals are unisexual. The probabilities of these results are $\frac{1}{8}$, $\frac{1}{64}$, and $\frac{1}{256}$ respectively.

As the hymenopteran sex determining mechanism does not automatically produce a primary sex ratio of 1 at conception, the observation of such a sex ratio at emergence is surprising for at least two reasons. Firstly, all recessive lethal alleles, immediately they arise by mutation, must kill all haploid (i.e. male) embryos into which they segregate. Secondly, one would expect the females to be more exposed to predation than males during both their frequent loaded flights over standardised paths, and their preoccupied pauses working on the two small areas of the quarry and the nest. This would be expected to have produced a selection pressure in solitary wasps with highly evolved maternal behaviour patterns which would have resulted in an excess of females in fertilized eggs such as is observed in even the most primitive social species in which the worker caste is not discretely specialized. That such an excess is not observed or, more correctly, that equality itself has been evolved, suggests that some premises should be re-examined (See Jayakar & Spurway 1966 a & b). Dutt (1913) reported that *madraspatanum* has not been discovered in the gut contents of any predator. Both species would be considered aposematic, but no more so than many social species which are known to be predated. Is there a com-

pensatory selection on males? The evolutionary consequences of 'protarrhenotoky' have been briefly discussed by Jayakar (1963).

SEASON AND DIAPAUSE

Table 1 and its footnote list all animals seen associated with a construct in our locality. The few isolated individuals we have seen do not extend the seasons of these species, determined either by when they were seen working or when they emerged in our collection.

There are unaccountable disappearances of both species e.g. the absence in 1964 of *madraspatanum* which was seen that year in both the more urban Calcutta locality, and on the as yet completely undeveloped river bank at Tikerpara, Dhenkanal. However, it seems that *esuriens* is not active during December and January and *madraspatanum* for a shorter period i.e. these species disappear for a 'winter' like their relatives in temperate climates. However we have only discovered diapausing individuals in the latter species.

Table 17 gives the dates of pupation and emergence (from pupae, not cells) of the offspring of *m4* and *m5*. The nests were dissected on 4/11 and 3/1 respectively when it was thought that all the inmates would

TABLE 17

PARTICULARS RE. OFFSPRING OF *S. madraspatanum* WASPS, *m4* AND *m5*

	laid	defaecated	died	pupated	died	emerged	sex
<i>m4</i> 1	on or before 18/10	—		26/2		6/3	♂
II	18/10		5/3				
III	18/10			25/2		6/3	♂
IV	19/10		5/3				
V	19/10		17/12				
VI	20/10			25/2		6/3	♂
VII	27/10	5/11		28/2	5/3		
VIII	28/10	6/11	12/11				
IX	30/10	7/11	21/12				
<i>m5</i> 1	10/12			10/3		19/3	♂
II	11/12			2/3	12/3		♀
III	11/12			<3/1		16/1	♀
IV	12/12			28/2		11/3	♀
V	14/12			4/3	12/3		♀
VI	on or before 15/12			28/1		10/2	♀
VII	before 17/12			2/3		11/3	♀
VIII	„			28/2		10/3	♀

The date of death is given in the space between the two relevant stages.

have at least ceased feeding and perhaps pupated. Only one, *m5 II* had pupated by 3/1 and this was not the earliest laid. He emerged on 16/1 after a preimaginal life of 36 days, compared with the 20 days recorded for the offspring of *m1* in July. Therefore it is likely that this individual is to be classified with his sibs as undergoing diapause.

There seems little doubt that all survivors of these two families laid late in the year underwent a diapause. This, as is usual in the group, was undergoing at the end of the last larval instar after feeding had ceased and defaecation had been performed.

It is curious that diapausing larvae should have started pupating before January 3. The range is over 67 days (<3/1-10/3) with a peak involving both families between 25/2 and 4/3. Jayakar & Spurway (1965a) have recorded similar data for *Chalybion bengalense* (Sphecoidea) and *Antodynerus flavescens* var. (Vespoidea) which show that both these species pupate after a diapause which extends well into the summer (May to July). Further observations show that *Chalybion bengalense* comes out of diapause in two bursts, a small one in January and a larger in May to July. There may, of course, be a corresponding second burst in the summer for *madraspatanum*, which we have not yet observed.

Despite the larger samples, we have *no* evidence for diapause in *esuriens*. Rouband (1916) takes for granted that some *Eumenes* species migrate during a dry season to regions with constant water. We may be accumulating evidence that *esuriens* migrates, perhaps southwards, during the coldest months of the year. An alternative suggestion is that the population becomes so much smaller that we have not yet recorded a specimen during this period, perhaps simply because the animals work less rapidly at the lower temperatures. Finally, fertilized females may hibernate as do females of the social wasps in temperate climates, and as *Polistes olivaceus* does even as far south as Calcutta.

COMPARISON BETWEEN INDIVIDUALS AND SPECIES

Table 18 ranks the various working speeds of the four *esuriens* watched in detail using the data presented in previous tables. From this table, *e2* appeared to perform most jobs more rapidly than the others and *e5* more slowly. This is confirmed by their mud fetching times graphed in Fig. 9. *e5* worked at the coolest period of the year but the temperatures for *e2* were only slightly higher, and lower than those for *e1* and *e8*. Therefore *e2* seemed more energetic than *e5*. She also used more loads during both her periods of *inphase* daubing and during her *crépissage* (Table 11), though this covered a surface of comparable area in both constructs. She perhaps also used more loads in cell construction (Table 2).

From the dates and location of the nests it is possible that *e2* and *e5* were the same wasp. The differences in their speed of work do not con-

TABLE 18
COMPARISON OF WORK SPEED IN *esuriens* INDIVIDUALS

	data from table	<i>e1</i>	<i>e2</i>	<i>e5</i>	<i>e8</i>
<i>On walls</i>	3	1	2	4	3
		2	1	4	3
<i>On lid</i>	10	1	3	4	2
		1	3	4	2
<i>On daub</i>	11	4	1	2	3
		3	1	2	4
<i>On panic daub</i>	11	+	1	2	3
		+	1	2	3
<i>On crépissage</i>	11	+	1	2	+
		+	1	2	+
<i>Away prey</i>	6	3	2	4	1
		3	2	4	1
<i>On prey</i>	7	2	4	3	1
		2	4	3	1
<i>Away inspection</i>	12	2	1	3	4
		2	1	3	4
<i>On inspection</i>	13	2	1	3	4
		4	1	2	3

1 the quickest work on the evidence provided by means.
1 on the evidence provided by medians.

tradict this possibility, as we have seen different work tempos in the same individual of *E. e. conoideus* when working on different constructs. Also, the observation that *e2* and *e5* seemed to have different water and mud sources is again not evidence for their separate identity as we have seen an *E. p. pyriformis* change her water source when beginning a second group of cells in a new place.

The daubing of the previous construct by *e1* before provisioning the naked open cell has not yet been noticed in any other *Eumenes* wasp.

As it was only observed twice, it may not reveal a consistent idiosyncrasy of behaviour.

If these four wasps and *m1* are typical of their species, the vespoid seems more efficient than the sphecoid. For the analogous chores, pot building, provisioning, and sealing, *esuriens* wasps achieve a comparable result with fewer loads than a *madraspatanum*. This economy, like their capacity to return with the appropriate loads after longer absences, is harmonious with the morphological conclusion that the vespoids are a more advanced group than the sphecoids.

DISCUSSION

For two centuries the behaviour of the Hymenoptera has been studied—and studied by some of the greatest biologists of whom we have historical record. These insects were often discussed as providing the most typical examples of instinctive behaviour. And by the criteria of species specificity and of performance without any previous apprenticeship (which are not two criteria but one), construction, predation, and other rearing activities of our wasps can be judged to be instinctive. We know of three systematic attempts to analyse the behaviour of members of the Aculeata influenced by the concepts of instinct due to Lorenz and Tinbergen (L-T), those of Deleurance (*e.g.* 1957), Tsuneki (*e.g.* 1958), and Evans (*e.g.* 1966).

These studies, and our own observations, completely vindicate Lorenz's emphasis that an instinct is best defined by motor patterns. They also vindicate his division of these motor patterns into *Erbkoordinationen* (or fixed action patterns) and taxis components. Because wasps make material artifacts, we are able to see that taxis components are typical of the homeostatic capacities that are characteristic of living creatures. The taxis components are necessary for a wasp to be able to build a species-specific nest on an individual location with special, theoretically unique, features by means of movements which are at least species-specific and often characteristic of much larger taxa.

We have described elsewhere (Jayakar & Spurway 1965b) the failure of two individuals of *E. emarginatus conoideus* to oviposit on finishing their cells and their different subsequent behaviour. One (*c3*) continued normally. The other (*c12*) seemed unable to stop building and so constructed a pathological nest. Wasp *c12* thus behaved as did Tsuneki's *Bembix niponica* and showed that the reproductive sequence is divided into sub-sequences of activities each of which is ended by a consummatory activity without which the next sub-sequence cannot be initiated, and after which, Tsuneki showed experimentally in his sphecoids, they cannot return to an earlier sub-sequence. This pattern of nervous organisation is characteristic of vertebrate instincts as L-T describe them. However

the behaviour of *c3* reveals that in wasps there is some variation in this organisation which may make possible an escape from its rigour.

If the motor pattern of the wasps' behaviour is harmonious with the L-T analysis, and the neural organisation sometimes so, the sensory aspects seem to be much less so. The fact that we have not performed experiments on our wasps would not have prevented us from gathering information on these matters if the information had been in the form in which it is revealed in vertebrate behaviour. We have been using a technique which L and T have themselves emphasised as being very fertile—observing the behaviour of animals surrounded by, and utilizing human artifacts. We have observed, as do all observers, the inevitable mistakes and miscarriages that such animals make, and we have observed their reaction to the inevitable interferences or frustrations which such animals invariably encounter. The technical vocabulary of L-T does immediately leap to the mind while watching mistakes being made, and frustrations being reacted to, by vertebrates. But this vocabulary does not leap to the mind while watching wasps which, as previous observers have noted, are much more succinctly described in human terms. A wasp making a mistake resembles much more a man entering the wrong house or, having forgotten where he put down his book, than a fledgling sparrow trying to perch on a horizontal high-light on a motor car or, among insects, a butterfly alighting on a coloured fabric while flying between flowers.

No reaction, usual or unusual, has suggested to us any hypothesis about the *sign stimuli* relevant to these wasps. Judging from the animals' movements, among the most important of these for building are those perceived tactilely by the antennae. The scanning movements differ in the two species. It is always difficult to recognise stimuli to senses which the observer does not share but, for example in work on the courtship of many insects, sign stimuli have been recognised, or at least models have been presented that provided sign stimuli. We, on the other hand, have seen neither a mistake in the putting down of a load, nor a pause that suggested that a sign stimulus was attended, but had not yet arrived. The ceaseless antennal probing can be described as *appetitive behaviour*, but the form of this seeking gives us no reason to classify the stimuli which it collects into two classes, of which one precipitates an instinctive action, and another which gives immediate information about the present state of the construct, and is relevant to the special features of the work. A wasp may put down a load on an obvious imperfection, or she may put it down completely isolated only to be joined up many loads later. We have not been able to recognise any evidence of an *innate releasing mechanism* common to these acts.

The much more thorough experimental analyses of Tsuneki confirm us in this matter. In his work on *Bembix niponica*, he is able to describe

the context which, on L-T instinct theory, must present the sign stimuli (or releasing factors) evoking the next sequence of movements. However, these contexts are only described in terms of their biological function e.g., 'burrowing ground', 'paralysed prey', 'operated prey', 'stored prey.' This is unsatisfactory. A sign stimulus can be presented and be effective quite *independently* of its normal context, *and it is identified by this experimental technique.* In William James's metaphor, we have never seen a wasp reacting to a label independent of its usual parcel.

However, c12 also showed a classic characteristic of instinctive reactions to sensory stimuli. As her nest became deformed she made a bad job worse because she reacted to certain features *only* when the stimuli these produced were relevant in the *normal* sequence. In an unusual context, objects, though undoubtedly perceived, were unable to stimulate a modification of behaviour, i.e., they presented no sign stimuli, as the wasp possessed no appropriate innate releasing mechanism to be stimulated. There is every reason to believe that *esuriens* and *madraspatanum* would show similar nervous organisation.

We have seen two members of *E. emarginatus conoideus* (Jayakar & Spurway, 1965b) and an individual of *Polistes olivaceus* put down preliminary loads before constructing their first cells as has been described for e11 and e22. Therefore abortive building is a typical activity of vespoids at least. Can it be regarded as parallel to the *intention movements* with which, for example, birds make abortive nest building attempts? This identification is fertile, but cannot, we think, be made without qualification. Does it justify the induction that nesting is controlled by a 'reproductive drive' (potentially describable in chemico-physiological terms) which gradually develops and/or accumulates in the individual animal as any other physical product may gradually increase; and when present in quantities inadequate to produce functionally efficient activities, produces small dissociated scraps of activity? The actual physical movements with which wasps make the abortive brackets and pedicels are in every way normal in form, intensity, and therefore, (at least temporarily) efficiency. They are associated with long periods of feeling which we have recognised as appetitive behaviour. They are not therefore like the intention movements of vertebrates, which are slight, languid, short, and have only traces of their typical form. The abortive behaviour of wasps resembles much more the early sketches of books or pictures on which some artists spend much thought, excitement, and effort before they determine on the final form. The tendency to make false starts may be as much a common idiosyncrasy among wasps as it is among men. If the two kinds of behaviour, i.e. the vertebrate languor and half-heartedness in performance and the wasp's lack of persistence with a particular construct (not lack of persistence with the performance of the activity) are interpreted as evidence for a physiological state in the

creatures concerned sufficiently alike for the same technical term (e.g. 'low motivation' or 'weak drive') to be applied, the differences between the two kinds of activity equally reveal that there are considerable differences between the nervous organisations of mechanical work which the drives activate.

The only obviously bad workmanship we have seen in these two species was the desertion of a partially built cell by *e4* and *m3*. *e21* had presumably put down the two orientated brackets 7 cm. from her first definitive cell. This may be a third example or may be more comparable to the abortive brackets just discussed. Roubaud (1916) discussed in detail many inefficient practices which he has observed in the African *Eumenes tinctor*. In discussing these, he approaches very closely a Tinbergian point of view, attributing them to various responses to the difficulty in finding provisions during the season in which they occur. Roubaud's wasps, in addition to laying extra eggs which we have previously discussed, sealed these extra eggs in cells without provisions. This he interprets as due to their inability to delay too long the performance of one part of the normal sequence because environmental conditions have prevented a previous phase from being completed or consummated. Roubaud has also seen wasps who went into periods of continuous cell building and plastering which he interprets as neurotic behaviours consequent on the frustrations of failing to find prey for provisions. In this he approaches very closely the Tinbergian idea of *displacement activity*.

The delays which we observed in our animals were caused by rain. As we have emphasised, these produced no sign of disturbance in the normal and functionally efficient sequence of activities. The wasps, on return, examined their construct and continued with the efficient task. Some delay in beginning again, and consequent repeated inspections, was sometimes observed, and may be attributed to waiting for the relevant drive to develop. If we accept this hypothesis, we are again saying that 'drives' in wasps are integrated with the other nervous functions in a different way from that in which they are hypothesised to be integrated in non-human vertebrates. On any hypothesis, wasps seem much less slaves of their drives—they almost invariably do what the external occasion demands, not what their internal physiological condition demands.

Both *e2* and *e8* did some daubing out of their usual sequence of activities. On one occasion *e8* carried out this daubing in the middle of building a cell. On all other occasions, it was hunting that was interrupted; *e1* did daub after building a cell but she did this for both cells that she was observed building. Although this 'out-of-sequence' daubing did not have any function obvious to us, it cannot be labelled as an inefficient activity.